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INTERACTIONS BETWEEN COYOTES AND RED FOXES IN YELLOWSTONE NATIONAL PARK, WYOMING

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Interactions between coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) indicate that coyotes often tolerate foxes, and yet at other times, are aggressive and kill foxes. The frequency and context in which coyotes are aggressive or tolerant of foxes are unknown. We observed 66 interactions between coyotes and red foxes in Yellowstone National Park, Wyoming, from February 1991 to April 1993. Foxes were deterred, displaced, or tolerated by coyotes in 17, 30, and 53% of the encounters, respectively. Deterrence and displacement of foxes by coyotes occurred at a similar frequency in the absence and presence of an ungulate carcass. Tolerance of foxes by coyotes occurred most frequently in the absence of a carcass. A group of coyotes feeding or resting at a carcass was a deterrent to approaching foxes.

Key words: *Canis latrans*, coyote, *Vulpes vulpes*, red fox, displacement, deterrence, tolerance

Coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) are distributed widely throughout North America (Nowak, 1991). Where the two canids occur sympatrically, territories of foxes tend to be on the periphery or outside of territories of coyotes, indicating spatial avoidance (Harrison et al., 1989; Major and Sherburne, 1987; Sargeant et al., 1987; Voigt and Earle, 1983). Interference competition was suggested as the cause of spatial segregation between coyotes and foxes. Few observations of interspecific encounters between coyotes and red foxes exist. Dekker (1983) reported nine instances of coyotes chasing red foxes in central Alberta. Sargeant and Allen (1989) received 42 accounts of interactions between coyotes and red foxes, in which 30 described aggression by coyotes toward red foxes, but only four described tolerance. Seventeen encounters were of foxes killed by coyotes while the fox was in a trap or snare. While accounts of encounters between coyotes and foxes described types of

interactions that occurred, frequency of interactions and context of occurrence were unknown.

We observed 66 interactions between free-ranging coyotes and foxes during late winter 1991–1993 in Yellowstone National Park. We examined number and behavior of the animals involved, distance between individuals, duration of interaction, social status of the coyote, and presence or absence of an ungulate carcass and the effect on the outcome of interactions between coyotes and red foxes.

MATERIALS AND METHODS

Observations were made in the Lamar River Valley, Yellowstone National Park, Wyoming (44°52'N, 110°11'E; elevation ca. 2,000 m) as part of a study that examined foraging and use of carcasses by coyotes. Habitats on the study area included forest, grassland, upland sage, sage-grassland, riparian, mesic meadow, and mesic shrub-meadow (modified from descriptions by Despain, 1990). We identified (by radiocollar, intraperitoneal implant, or unique pel-

age characteristics) 23, 34, and 41 coyotes from five resident packs in the study area during the winters of 1990–1991, 1991–1992, and 1992–1993, respectively and two, two, and seven foxes during the same winters, respectively.

Interactions were observed with a spotting scope of 15–30× magnification from a vehicle or vantage points on hills overlooking the valley. Observations occurred throughout the valley, but were within the boundaries of territories of the five resident packs of coyotes. For an encounter to be counted, the distance between a coyote and fox had to be <500 m, and one of the individuals had to notice the presence of the other species. For each encounter, we recorded number of foxes and coyotes involved, behavior of foxes and coyotes immediately preceding the interaction, estimated distance between individuals at initiation of an interaction, duration of interaction, presence or absence of an ungulate carcass (elk, *Cervus elaphus*, or mule deer, *Odocoileus hemionus*), social status (if known) of coyotes, and outcome of interaction. Categories of behavior included traveling, resting, hunting small mammals, and feeding on a carcass (Beckoff and Wells, 1981). If a group of coyotes was involved, estimated distance was the distance between the fox and closest coyote in the group. We examined the social status of the coyote for interactions when only one coyote was involved. Social status was categorized as alpha (dominant, breeding individual), beta (subordinate to alphas, dominant over young), or young (offspring that were subordinate to both alpha and beta coyotes) based upon separate hierarchies of dominance for males and females that were observed within each resident pack (Mech, 1970; Rabb et al., 1967; Schenkel, 1947, 1967).

We classified outcomes of interactions between coyotes and red foxes as deterrence, displacement, or tolerance. Deterrence was recorded when the presence of coyotes caused the fox to avoid the immediate area (i.e., the fox changed direction of travel and moved away from the coyote), or when the fox would not approach and feed on a carcass. Deterrence started when one species noticed the presence of the other, whereas it ended when either one canid moved >500 m from the other, one canid was no longer visible to the other, the coyote displaced the fox, or darkness precluded further observation. Displacement occurred when one or more coyotes approached or chased a fox caus-

ing the fox to move away from the immediate area or carcass. A displacement ended when the coyote stopped its approach or chase of the fox. Tolerance was recorded when coyotes appeared to ignore a fox and started when one species noticed the presence of the other, whereas it ended when either one canid moved >500 m from the other, one canid was no longer visible to the other, the coyote displaced the fox, or darkness precluded further observation. Our focus was to understand how coyotes responded to foxes; therefore, only coyotes could deter, displace, or tolerate foxes, not vice versa. However, we observed no interactions that would suggest that foxes displaced or deterred coyotes. Sargeant and Allen (1989) reported only one encounter that described defensive behavior by a fox toward a coyote.

We used a *G*-test to analyze the frequency of outcomes in the presence and absence of a carcass, and frequency of outcomes among social classes of coyotes (Zar, 1984). We then partitioned the *G*-value to detect where the differences were that contributed to the overall significant test statistic. We tested for differences in number of foxes and coyotes, distance, and duration with one-way analysis of variance followed by a Tukey's test using the software program SYSTAT (Wilkinson et al., 1992).

RESULTS

We observed 66 interactions between coyotes and red foxes from February 1991 to April 1993; two interactions occurred in winter 1990–1991, three in winter 1991–1992, and 61 in winter 1992–1993. Most observations occurred in the last winter due to an increase in the number of foxes in the valley and to an increase in the monitoring of carcasses. Of the 66 occurrences, 36 were associated with activities of coyotes and foxes at a carcass and 30 were recorded in the absence of an ungulate carcass (Table 1). Deterrence, displacement, and tolerance were observed in 22, 44, and 33% of the interactions near a carcass, respectively. Deterrence, displacement, and tolerance were the outcome in 10, 13, and 77% of the observations, respectively, in the absence of a carcass. The outcome of interactions between coyotes and foxes

TABLE 1.—Types of interactions and behavior immediately preceding 66 encounters between coyotes and red foxes in Yellowstone National Park, Wyoming, during 1991 to 1993, when an ungulate carcass was present or absent.

Behavior	Carcass present			Carcass absent		
	Deterrence	Displacement	Tolerance	Deterrence	Displacement	Tolerance
Red fox						
Travel	3	2	1	3	3	14
Rest	4	2	2	0	1	3
Hunt	1	0	0	0	0	6
Feed on carcass	0	12	9			
Coyote						
Travel	0	15	1	3	2	8
Rest	3	0	9	0	2	11
Hunt	0	0	1	0	0	4
Feed on carcass	5	1	1			

differed in the presence and absence of an ungulate carcass ($G = 13.1$, $d.f. = 2$, $P < 0.005$). Coyotes were more tolerant of foxes in the absence of a carcass than in the presence of a carcass ($G = 12.9$, $d.f. = 1$, $P < 0.001$), whereas no difference was found for deterrence and displacement of foxes by coyotes when a carcass was present or absent ($G = 0.2$, $d.f. = 1$, $P > 0.50$). We observed that resting and traveling coyotes typically were tolerant of active foxes when no carcass was present. When a carcass was present, we observed that coyotes traveling toward a carcass usually would displace foxes that were feeding on the carcass. Coyotes resting near a carcass often tolerated a fox feeding on the carcass. We found that alpha, beta, and young coyotes similarly deterred, displaced, and

tolerated foxes in the presence or absence of an ungulate carcass (presence: $G = 0.8$, $d.f. = 4$, $P > 0.90$; absence: $G = 6.0$, $d.f. = 4$, $P > 0.10$).

When a carcass was present, we found that the number of foxes involved in the interaction did not differ among the three outcomes (Table 2; $F = 0.30$, $d.f. = 2,33$, $P > 0.70$). In contrast, the number of coyotes involved in the interaction did differ among the three outcomes when a carcass was present ($F = 16.69$, $d.f. = 2,33$, $P = 0.0001$). Coyotes were in larger groups when they deterred foxes ($P < 0.001$), but groups were similar and smaller when coyotes displaced or tolerated foxes ($P > 0.20$). We found that in the absence of a carcass, neither the number of foxes, nor the number of coyotes involved in an interaction dif-

TABLE 2.—The mean (\pm SD) number of foxes and coyotes interacting, distance (m), and duration (min) of 66 encounters between coyotes and red foxes in Yellowstone National Park, Wyoming, during 1991 to 1993, in the presence and absence of an ungulate carcass.

Observation	Carcass present			Carcass absent		
	Deterrence	Displacement	Tolerance	Deterrence	Displacement	Tolerance
Foxes	1.2 \pm 0.5	1.2 \pm 0.4	1.5 \pm 1.4	1.0	1.0	1.0 \pm 0.2
Coyotes	5.6 \pm 2.8	1.1 \pm 0.3	2.2 \pm 2.2	2.7 \pm 1.5	1.2 \pm 0.5	1.4 \pm 1.3
Distance	113 \pm 108	25 \pm 18	57 \pm 112	217 \pm 76	82 \pm 54	242 \pm 141
Duration	172.0 \pm 134.6	1.1 \pm 0.3	46.8 \pm 50.6	2.7 \pm 2.1	3.7 \pm 2.7	20.6 \pm 35.1

ferred among the three types of outcomes (foxes: $F = 0.14$, $d.f. = 2,27$, $P > 0.80$; coyotes: $F = 1.38$, $d.f. = 2,27$, $P > 0.25$). When a carcass was present, mean distance between the two canids differed among the three outcomes ($F = 3.03$, $d.f. = 2,33$, $P = 0.06$). Coyotes displaced foxes at a shorter distance than when they deterred foxes ($P = 0.05$), but the distance was not different than when coyotes tolerated foxes ($P > 0.50$). The distance between the two canids was similar when coyotes tolerated and deterred foxes ($P > 0.25$). Mean distance between the two canids did not differ among the three outcomes when no carcass was present ($F = 2.56$, $d.f. = 2,27$, $P = 0.09$). Mean duration of an interaction between coyotes and foxes was different among outcomes when a carcass was present ($F = 15.22$, $d.f. = 2,27$, $P = 0.0001$). The duration of an interaction was longest when a coyote deterred a fox ($P < 0.003$), but similar in length when coyotes displaced or tolerated a fox ($P > 0.10$). The duration of an interaction was not different when coyotes deterred, displaced, or tolerated foxes in the absence of a carcass ($F = 0.80$, $d.f. = 2,27$, $P > 0.40$).

DISCUSSION

Observations of encounters between coyotes and red foxes are rare because both canids typically are nocturnal, secretive, and spatially segregated (Harrison et al., 1989; Kleiman and Brady, 1978; Sargeant and Allen, 1989). Most observations of interactions between these canids indicate that coyotes were aggressive toward foxes (Sargeant and Allen, 1989), whereas no reverse aggression by foxes toward coyotes was reported. Foxes appeared to be aggressive only when attacked or defending offspring at a den. In our study, coyotes displaced a fox from the immediate vicinity or from a carcass in 30% of the encounters. In contrast, 53% of encounters of coyotes and foxes resulted in coyotes tolerating foxes in close proximity. In the absence of an ungulate carcass, coyotes were aggressive to-

ward foxes in only 13% of encounters, whereas aggression occurred in 44% of encounters when a carcass was present. Coyotes were more tolerant of foxes in the absence of an ungulate carcass (77%), than when a carcass was present (33%). Intraspecific competition at a carcass occurred among members of a pack of coyotes (Gese, 1995), hence reduced interspecific tolerance of foxes by coyotes near a carcass was not surprising. However, the observations of tolerance of foxes by coyotes, both near a carcass and within the territory of a pack of coyotes, was significant when compared to previous reports about interactions between coyotes and foxes. Wolves (*C. lupus*) also were tolerant of foxes in their territory and near carcasses (Murie, 1944). Conversely, wolves have been observed to kill red foxes (Mech, 1966).

The number of coyotes present and their behavior before the encounter influenced the outcome of the interaction. When a carcass was present, foxes were deterred more often by a group of coyotes than by a single coyote. A group of coyotes resting or feeding at a carcass was a deterrent to a fox approaching the carcass. A group of coyotes may be more likely to detect and pursue a fox than a single coyote. The presence of a carcass also concentrated a high number of coyotes in a focal area, possibly increasing the risk of predation to a fox. A single coyote approaching a carcass readily displaced foxes, but also was tolerant of foxes at the carcass when the coyote was resting near the carcass.

While we observed interspecific tolerance, we still recognize that only one aggressive encounter with a coyote can result in the death of the fox. Coyotes can kill foxes (Sargeant and Allen, 1989), hence the behavior of the coyote likely dictates whether it tolerates the presence of a fox. We found that in 71% of our observations, coyotes resting near a carcass had fed on the carcass before an interaction with a fox. Coyotes that displaced a fox from a carcass proceeded to feed in 67% of the

cases. If a coyote recently has fed on a carcass, the coyote likely would be resting and may be tolerant of a fox at the carcass. In contrast, a hungry coyote would likely displace a fox from a carcass, and deter the fox from approaching until the coyote had finished feeding. Among African carnivores, the amount of food consumed by the dominant species greatly influenced the level of tolerance exhibited toward other carnivores at a carcass (Kruuk, 1972; Schaller, 1972).

Our results are significant because we were able to observe the frequency of different outcomes between coyotes and red foxes, as well as collect detailed information about each encounter. In contrast to previous studies documenting spatial avoidance of coyotes by foxes, our observations indicate that coyotes will tolerate red foxes in their territory and at a carcass. The numerous prey (ungulates and microtines) available within the Lamar Valley during the three winters may have influenced the level of interspecific tolerance observed between coyotes and foxes. Perhaps, in other areas or during years of low abundance of prey, competition for resources would be more intense and interspecific aggression by coyotes toward foxes consequently would be higher, resulting in spatial avoidance of coyotes by red foxes.

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